

A New Species of the Genus *Lile* (Clupeiformes: Clupeidae) of the Eastern Tropical Pacific

José Luis Castro-Aguirre¹, Gorgonio Ruiz-Campos² and Eduardo F. Balart³

¹*Centro Interdisciplinario de Ciencias Marinas, I.P.N. Departamento de Pesquerías y Biología Marina, Apdo. Postal 592, La Paz, Baja California Sur 23001 México.*

²*Universidad Autónoma de Baja California. Facultad de Ciencias, Apdo. Postal 1653, Ensenada, Baja California 22800 México.*

³*Centro de Investigaciones Biológicas del Noroeste, S.C. Laboratorio de Ictiología, Apdo. Postal 128, La Paz, Baja California Sur 23001 México.*

Abstract.—A new species of tropical sardine belonging to the genus *Lile* is described. The species differs from other known members of the genus by its morphometrics, morphology, number of gill rakers, coloration and distributional pattern. This new taxon represents the third known species of the genus *Lile* for the eastern tropical Pacific.

Resumen.—Se describe una especie nueva de sardina tropical que pertenece al género *Lile*. Difiere de los otros miembros de este género por su morfometría, morfología, número de branquiespinas, coloración y patrón de distribución geográfica. Ésta es la tercera especie, de este género, que se conoce en los litorales del Pacífico oriental tropical.

The Clupeidae, order Clupeiformes, is divided into five subfamilies. One of them, Clupeinae, contains 15 genera and almost 80 species widely distributed through temperate, subtropical and tropical seas of the world's oceans (Whitehead 1985). The genus *Lile* Jordan and Evermann 1896 of subfamily Clupeinae, is exclusive to tropical and subtropical waters of Middle and South America. Besides the new species described here, three other *Lile* species are known: (1) *L. stolifera* (Jordan and Gilbert 1882), with a disjunct distribution from Bahía Magdalena, Baja California Sur (BCS) and Golfo de California to northern Nayarit, México, and from Costa Rica to Perú; (2) *L. piquitinga* (Schreiner and Miranda-Ribeiro 1903) which inhabits the fresh and brackish waters of the Atlantic drainage of Venezuela and Brazil; and (3) *L. gracilis* Castro-Aguirre and Vivero 1990, known from Jalisco, México to Golfo de Fonseca, Honduras.

Methods

All body measurements and counts of fin rays, gill rakers, ventral scutes, and midlateral scales were taken based on Whitehead's methods (1985). Original morphometric data were transformed to thousandths of the cephalic length or standard length and descriptive statistics (mean, standard deviation, mode, and range) were computed. An analysis of discriminant function (Statistica 4.2 program) was used to identify the most important biometric characters to classify *Lile nigrofasciata* and *L. stolifera*.

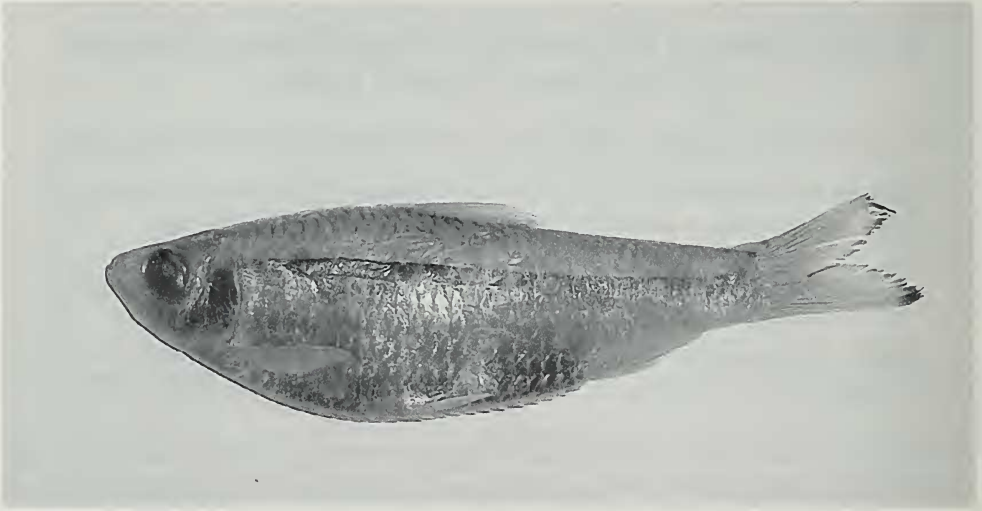


Fig. 1. Holotype of *Lile nigrofasciata* (CI: 2032), adult female, 104 mm SL, Bahía de Guásimas, Sonora, México. Photograph by Gorgonio Ruiz-Campos.

Abbreviations of the fish collections where the studied specimens are deposited are as follows: CI, Centro Interdisciplinario de Ciencias Marinas (CICIMAR, I.P.N.), La Paz, BCS; UABC, Facultad de Ciencias, Universidad Autónoma de Baja California, Ensenada, Baja California; ENCB-I.P.N., Departamento de Zoolo-gía, Escuela Nacional de Ciencias Biológicas, México, D.F.; CIB, Centro de Investigaciones Biológicas del Noroeste, S.C., La Paz, BCS; IBUNAM, National Fish Collection at the Instituto de Biología, Universidad Nacional Autónoma de México, México, D.F.; CAS, California Academy of Sciences, San Francisco, California, U.S.A.; and LACM, Natural History Museum of Los Angeles County, Los Angeles, California (cf. Other material examined in Appendix 1). Number of specimens examined is indicated in parenthesis.

Results

Lile nigrofasciata sp. nov. (Fig. 1).

Holotype.—CI: 2032, a female of 104 mm standard length (SL) from Bahía de Guásimas, Sonora, México, collected by E.F. Balart and A. Arreola Lizárraga, 23 Feb. 1996, at a depth of 1.5 m.

Paratypes.—CI: 2039 (1), 98 mm SL collected along with the holotype; IBUN-AM: P9520 (2), 96.0–100.0 mm SL, *idem*; CIB: 3001 (2), 93.1–94.5 mm SL, *idem*. CI: 1886 (50), 56.5–77 mm SL, Santispac, Bahía Concepción, BCS, collected by P.J.P. Whitehead, 29 Nov. 1988. CI: 4922 (35), 74.1–86.0 mm SL, Estero El Conchalito, Ensenada de La Paz, BCS, México, collected by A.F. González-Acosta, 18 Aug. 1997.

The results of the morphometric and meristic analysis are listed in the Table 1.

Diagnosis.—A species belonging to the genus *Lile*, with the following differential characteristics: body elongate, very compressed and high, its maximum depth 3.3 to 4.4 (mean = 3.7) times in standard length; dorsal and ventral profiles convex; 36 to 40 (mode = 38) gill rakers on lower limb of the first gill arch; 34

to 49 (mode = 40) midlateral scales; 14–18 (mode = 16) prepelvic scutes; 10–16 (mode = 12) postpelvic scutes; dorsal and anal fins with 13–17 (mode = 15) and 14–16 (mode = 16) rays, respectively; head relatively small, its maximum length 3.7 to 5.4 (mean = 4.2) times in standard length; body with a dark green (in life) or black (in alcohol) band extended from the supraposterior edge of the opercle to the final part of the caudal peduncle; iris black; pupil translucent, whitish or lightly gray; most of individuals examined have both tips of their caudal lobes with a black stain; color of the opercle in specimens <70 mm SL is gray-silver, and in those >80 mm SL with a dark gray or black stain.

Description.—Body elongate, fusiform, compressed, with dorsal profile arched and the ventral profile notably convex. Cephalic region spindle-shaped; mouth oblique, almost vertical. Head relatively small, its length 3.7 to 5.4 (mean = 4.2) times in standard length; eye large, its diameter 2.4 to 4.1 (mean = 3.0) times in cephalic length; preorbital distance shorter than eye diameter and contained 3.1 to 5.2 (mean = 3.9) times in cephalic length; postorbital distance longer than eye diameter and contained 1.9 to 3.2 (mean = 2.6) times in cephalic length. Posterior edge of opercle rounded and flat, not serrated, but with a concave notch on its post-distal part. Preopercle flat, its posterior edge straight, shallowly oblique and directed anteriorly where it connects with the rounded suborbital. A distinctive membranous structure on anterior edge of cleithrum that appears juxtaposed to first lateral scales, and covered with a great number of highly ramified complex tubules. Tubular system extended to nuchal region where it connects to other side of body by means of a tubular system. Two anterior fontanels located between supraocular and nuchal regions, distinguishable as two dark areas, also identified as a complex tubular system connected with those of the preopercle, opercle, and membranous structure. Mouth terminal, protrusible, forming a tubular structure composed of two supramaxillary bones, which are associated with the maxillary bone. Both sides of symphysis of lower jaw with several series of conical, blunt, minute teeth. Inner border of jaws without teeth; conical and unicuspidated teeth forming a conglomerate on the palatines. Tongue spatulate and lacking teeth. Six branchiostegal rays supported by flexible ligaments. Lower limb of the first gill arch with 36 to 40 (mode = 38) thin elongate gill rakers, closely approximated. The pseudobranch has from 13 to 14 relatively thick filaments. Body elongate, compressed, deep, maximum depth 3.3 to 4.4 (mean = 3.7) times in standard length; dorsal profile arched, ventral profile notably convex. The ventral scutes originate from the first scale behind the isthmus and finish before the anal pore; their numbers range from 14 to 18 (mode = 16) prepelvic and 10 to 16 (mode = 12) postpelvic or preanal. Origin of dorsal fin situated before that of the pelvic fins and closer to tip of mouth than to base of caudal peduncle. Dorsal fin length is almost equal to the cephalic length; dorsal rays from 13 to 17 (mode = 15), the last two rays highly ramified. Pectoral fins relatively small, falciform, their length almost equal as the cephalic length; insertion of pelvic fins begins at post-distal part of gill opening and above the thoracic border. Pelvic fins small, their maximum length 1.6 to 2.5 (mean = 1.9) times in cephalic length, and 8 branched rays. Anal fin short, not very high, with a scaly sheath, and 14 to 16 rays (mode = 16), the last two rays branched; anal fin situated at posterior one-third of the body. Caudal fin forked, 5–11 upper procurrent rays, 10 upper principal rays (9 of them forked), 9 lower principal rays (8 of them forked), and 6–9 lower pro-

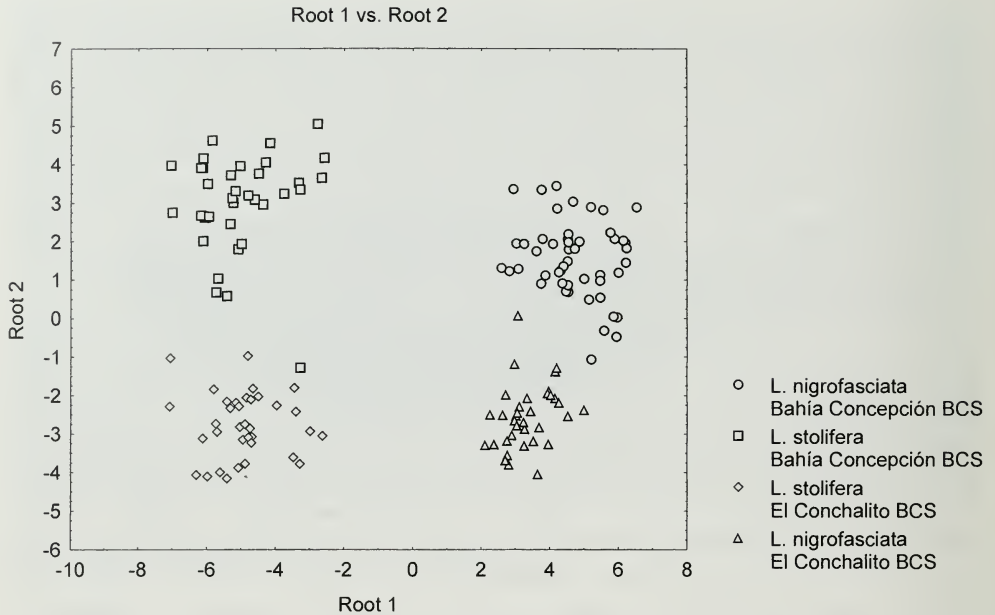


Fig. 2. Discriminant function analysis of populations of *Lile* spp. in the Gulf of California, México. Axis 1 vs. Axis 2. Pooled data.

current rays. Scales large, somewhat deciduous, with smooth border, four continuous grooves and one discontinuous of central position, the nearest groove to the lower border has the form of an arch, the other cross the entire scale. Number of scales in lateral series varies from 34 to 49 (mode = 40); predorsal scales 11–13. Total vertebrate 40–41 (mode = 41), 14 or 15 (mode = 15) caudal. Predorsal bones (=upperneurals) between cranium and the first dorsal finrays 9–11 (mode = 11). Caudal complex with two (60%) or three (40%) epurals.

Biometric Analysis.—Twenty-one biometric variables of 85 examined specimens of *Lile nigrofasciata* and 71 *L. stolifera* were analyzed. Wilks' Lambda values varied from 0.0027 to 0.0204, suggesting a strong discrimination between the species (Wilk's Lambda for all variables combined: 0.00273, approx. $F_{(63, 394)} = 39.010$, $p < 0.0000$). The values of tolerance ranged between 0.4974 and 0.9002. The classification matrix obtained here indicates that 100% of the examined individuals were correctly classified for the populations of *Lile nigrofasciata* (Bahía Concepción and El Conchalito, BCS), as well as that of *L. stolifera* from El Conchalito, BCS. The specimens of *L. stolifera* from Bahía Concepción were correctly classified with an accuracy of 97.22%.

Only three of the 21 biometric variables analyzed contributed significantly to the discrimination of both species of *Lile*: interorbital distance ($p < 0.00001$), number of midlateral scales ($p < 0.00003$), and number of gill rakers on the lower limb of the first gill arch ($p < 0.00000$).

The squared Mahalanobis distances were significantly greater between populations of *L. nigrofasciata* and *L. stolifera*, but were not significant between populations of the same species, as shown in the graph of the discriminant function analysis (Fig. 2).

Coloration.—Living specimens, with the exception of the olive-green or black midlateral band, are yellowish-green and somewhat translucent in their predorsal region. The head is also yellowish-green, with a gray-silver spot on the preopercle and opercle as result of a great concentration of black pigment inside the branchial chamber. Gums and distal part of the lower jaw are black. The upper lip and internasal area are black or dark gray. The gill filaments are whitish or yellowish. The oral chamber is whitish. A distinctive black or dark line travels from the nape to the dorsal fin origin and to the precaudal area. The iris is black or dark gray, the pupil is whitish and translucent. In most individuals both caudal lobes are tipped black, although some of them have only the upper lobe with a faint black tip. Anal, pectoral, and pelvic fins are yellowish or whitish.

Habitat.—The holotype and five paratypes were caught in 1.5 m in Bahía de Guásimas, Sonora, near the town of the same name. This coastal lagoon, with anti-estuarine circulation and muddy-sandy bottom, is located at the geographical coordinates, 27°54' and 27°59' N, and 110°48' and 110°55' W. Water conditions at capture were: salinity, 45 ppt (annual range for 1996, 35–45 ppt), temperature, 20.5°C (annual range for 1996, 14–30°C), and Secchi disc visibility, 0.72 m. The dominant fish species at the type locality were *Ariopsis seemani*, *Anchovia macrolepidota*, *Mugil cephalus*, *Diapterus peruvianus*, *Anchoa* spp., *Eucinostomus* spp., and *Colpichthys regis*. The other paratypes from Bahía Concepción and Ensenada de La Paz (Manglar El Conchalito), BCS, were collected in shallow littoral areas with soft silt, and were usually associated with mangrove roots that border these coastal lagoons. The fish communities at both BCS sites were represented by the following dominant species: *Eucinostomus* spp., *Diapterus peruvianus*, *Anchovia macrolepidota*, *Mugil cephalus* and *Lile stolifera*. In addition, voucher specimens captured at oligohaline conditions (5.0–15 ppt) in the coastal lagoon of Tres Palos, Guerrero, México, were also examined. Other specimens of the new species were collected in the Oriental, Occidental, Inferior and Superior coastal lagoons, Oaxaca, as well as in the Mar Muerto, Chiapas, in salinities of ≥35.5 ‰. In these last five localities the fish composition is very similar, but *Lile gracilis* replaces to *L. stolifera*.

Etymology: The name *nigrofasciata* alludes to the obvious dark or black band that travels the midlateral part of the body, from the posterior edge of the operculum to the end of the caudal peduncle.

Key to the species of Lile of the eastern tropical Pacific

- 1. Midlateral band dark or black green; iris black; pupil translucent, dark gray or black; 36–40 (mode = 38) gill rakers on lower limb of the first gill arch *Lile nigrofasciata* (Fig. 3A).
Midlateral band silvery; iris yellow or golden-silvery; pupil black, not translucent; 24–32 gill rakers on lower limb of the first gill arch 2
- 2. Origin of dorsal fin located ahead of or on a vertical through the insertion of the pelvic fins; 27–42 midlateral scales in a longitudinal series; ventral profile notably convex; body depth 2.8–3.7 times in standard length; tips of both caudal lobes with conspicuous black blotches ... *Lile stolifera* (Fig. 3B).
Origin of the dorsal fin located behind the insertion of the pelvic fins; 34–36 midlateral scales in a longitudinal series; ventral profile slightly convex



Fig. 3. Comparison of the three species of the genus *Lile* of the Eastern Tropical Pacific. (A) *Lile nigrofasciata* sp. nov. (holotype, CI: 2032, 104 mm SL), Bahía de Guásimas, Sonora. (B) *Lile stolifera* (CI: 4738, 83 mm SL), Manglar El Conchalito, Baja California Sur. (C) *Lile gracilis* (ENCB-IPN: 7134, 71.4 mm SL), Mouth of Río Balsas, Guerrero. Photograph by Gorgonio Ruiz-Campos.

or straight; body depth 4.0–5.5 times in standard length; only the upper tip, if any, of the caudal fin with a faint dark mark *Lile gracilis* (Fig. 3C).

Geographical distribution.—Based on material examined deposited in the ichthyological collections previously mentioned, *Lile nigrofasciata* is distributed in the Bahía Magdalena-Bahía Almejas lagoon complex in the southwestern Baja California Sur, México, the Golfo de California (Bahía de Guásimas, Sonora; Bahía Concepción and Manglar El Conchalito at Ensenada de La Paz, BCS), and along the western coast of Mexico and Central America, to Colombia, Ecuador and northern Perú.

Discussion

The recognition of this new species is interesting from a systematic and biogeographic point of view. Its closest relationship is with *Lile stolifera*, based on

the position of the dorsal fin in relation to that of the pelvic fins, both species having the origin of the dorsal fin ahead of the insertion of the pelvics. This characteristic is also observed in the Atlantic species *L. piquitinga* (distributed from Venezuela to Brazil) but not in *L. gracilis* (distributed from the central Pacific of México to Honduras) whose individuals have the dorsal fin origin slightly behind the origin of pelvic fins (Castro-Aguirre and Vivero 1990). *L. stolifera* and *L. nigrofasciata* are distinguished by gill-raker numbers on the lower limb of the first gill arch, the first species with 24 to 31 (mode = 27), the second with 36 to 40 (mode = 38).

The size and form of the scales also different; *L. stolifera* has small scales (average maximum length 3 mm) in the form of a shield with their posterior edges smoothly convex; in contrast, the scales of *L. nigrofasciata* measure on average 5 mm in maximum length, and their posterior edges are angular with the sharp tips. The most conspicuous diagnostic characteristic is coloration; *L. stolifera* has a brilliant silvery midlateral band, golden-yellow or silvery-golden iris, black (no translucent) pupil. In comparison, *L. nigrofasciata* has a dark or black-green midlateral band, dark or black gray iris, and the translucent gray pupil. Both species share characters such as the numbers of scales in a longitudinal series, ventral scutes, and anal rays (Table 1), and filaments of the pseudobranch (12 to 14). Based on five cleared-and-stained specimens of both species, a preliminary osteological study revealed some interesting facts: whereas the total vertebrae number are almost the same in *L. stolifera* and *L. nigrofasciata* (41–42 vs. 40–41), the caudal vertebrae number is not. *L. stolifera* has 16 to 17 (16) caudal vertebrae and *L. nigrofasciata* has 14 to 15 (15). On the other hand, *L. gracilis* has 38 to 40 (38) total vertebrae number and 17 to 18 (17) caudal vertebrae number. In comparison, the Atlantic species *L. piquitinga*, has 38 to 41 total vertebrae and 14 to 15 caudal vertebrae (Gómez-Gaspar 1976). *L. stolifera* has 8 to 10 (9) predorsal bones, *L. nigrofasciata* 9 to 11 (11), and *L. gracilis* 8 to 9 (9), very near to *L. stolifera*, but the first bone of the series is larger than in the other species (Fig. 4). *L. piquitinga* has 7 to 8 predorsal bones (Gómez-Gaspar 1976; McGowan and Berry 1984). Two or three epural bones were observed in the caudal skeleton of *L. nigrofasciata* (Fig. 5), whereas in *L. stolifera* two epural bones is the most frequent situation (80%) and rarely three. Vivero and Romero-Castillo (1990) found two epural bones in *L. gracilis*; however, in very small specimens (e.g. 35.6 mm) three epural bones can be observed; in some the double character of the second epural bone is still evident. Some osteological studies have shown that in some species of Clupeiformes the fusion of one pair of epural bones is relatively common during larval development (Balart 1985; Matsuoka 1998).

The geographical ranges of both species also differ (Fig. 6): *Lile nigrofasciata* has a widespread distribution in the eastern tropical Pacific, while *L. stolifera* has a quasi-antitropical distribution. Both species are sympatric from Bahía Magdalena-Bahía Almejas coastal lagoon complex in the northwestern Baja California Sur and both coasts of Golfo de California to Bahía Banderas, Jalisco, México. The distribution of *Lile stolifera* is interrupted from northern Bahía Banderas, appearing again as sympatric with *L. nigrofasciata* from Costa Rica to Perú (Castro-Aguirre et al. 1999). *L. nigrofasciata* is also sympatric with *L. gracilis* from

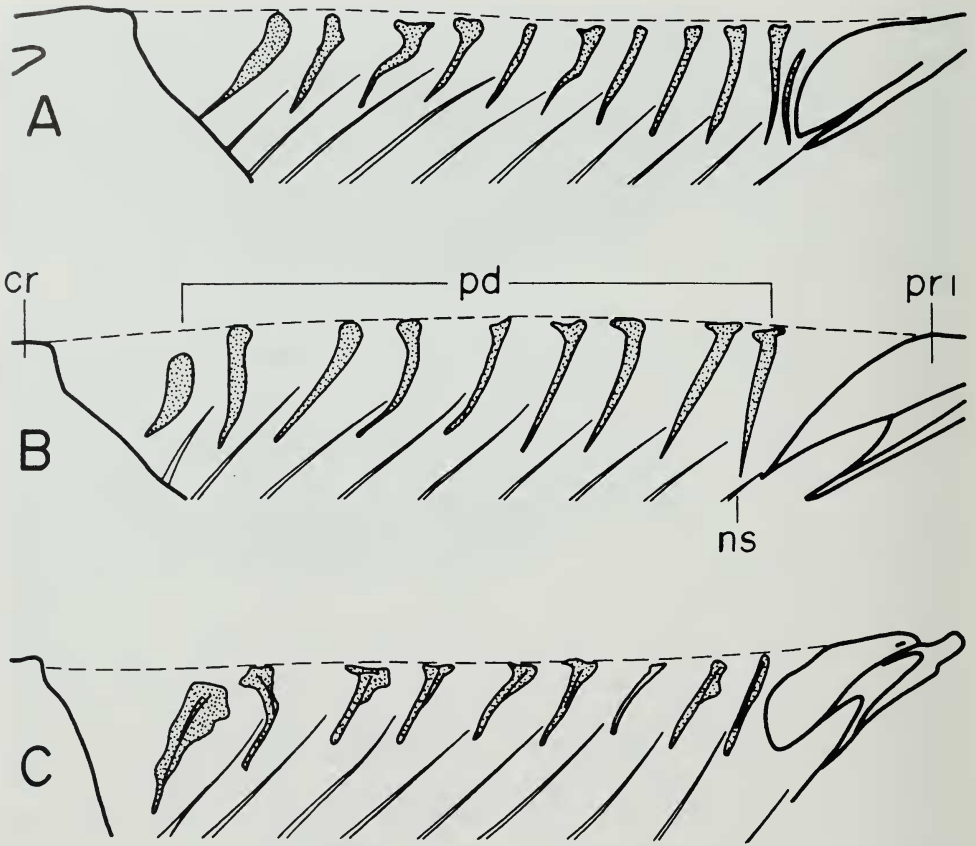


Fig. 4. Characteristic arrangement of predorsal bones (left lateral view) in Pacific species of *Lile*. (A) *L. nigrofasciata* sp. nov., (B) *L. stolifera* and (C) *L. gracilis*. cr, cranium; ns, neural spine; pd, predorsal bone; pr, proximal radial of dorsal fin support.

the Mexican central Pacific to Golfo de Fonseca, Honduras (S. Contreras-Balderas, unpublished data).

Photographs of specimens identified as "*Lile stolifera*" that were provided by Chirichigno (1963: 14, fig. 5) and Yáñez-Arancibia ("1978" [1980]: 266, plate 12, fig. 4) correspond to *L. nigrofasciata*.

It is not feasible to present a probable phylogeny of the genus because more detailed anatomical studies of the four nominal species are needed, particularly the osteology of the caudal complex and the neurocranium, as well as a comparative study of their early ontogenic stages. Based on some osteologic aspects of *Lile gracilis*, Vivero and Romero-Castillo (1990) proposed that the allopatrical processes led to the persistence of neotenic characters. It is necessary, however,

Fig. 5. Comparison of the caudal skeleton (left lateral view) of the three species of the genus *Lile* in the eastern tropical Pacific. (A) *L. nigrofasciata* sp. nov., (B) *L. stolifera* and (C) *L. gracilis*. a, radial cartilage; cp, preural centrum; e, epural; h, hypural; na, neural modified spine; o, opisthural cartilage; ph, parhypural; u, ural centrum; un, uroneural. Stippled areas, cartilage.

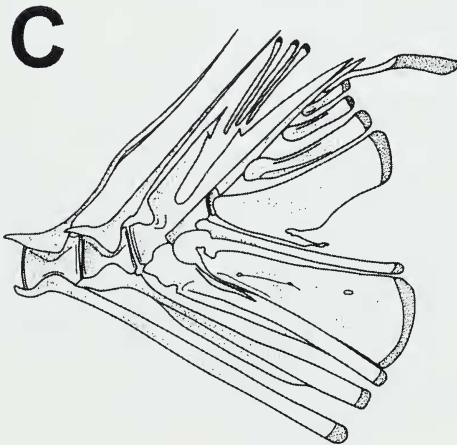
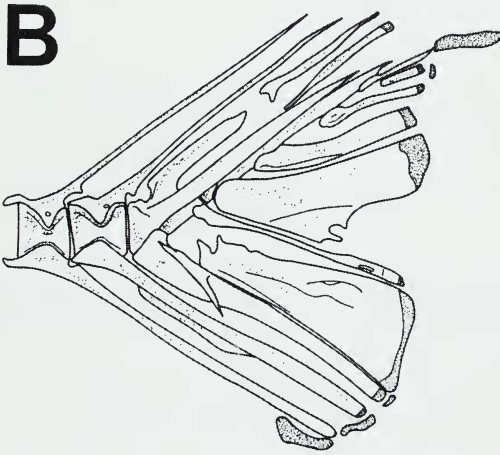
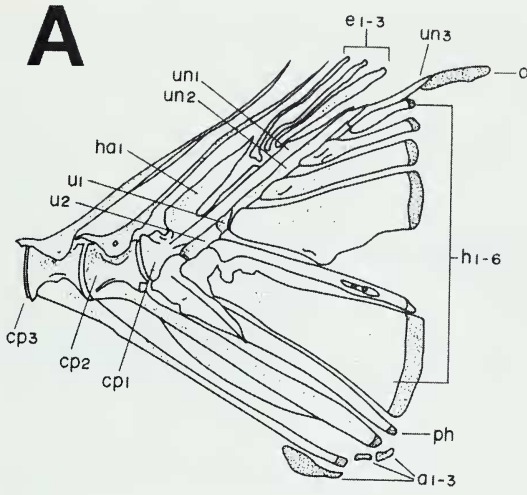


Table 1. Morphometry of *Lile nigrofasciata* sp. nov. and *L. stolifera*. Measurements according to Whitehead (1985).

	<i>Lile nigrofasciata</i> sp. nov. N = 85					<i>Lile stolifera</i> N = 71				
	Mean	Mode	Min	Max	s	Mean	Mode	Min	Max	s
Meristic measures										
Scales in lateral series	40	40	34	49	2.7	36	40	27	42	4.0
Gill rakers on lower limb of the first gill arch	38	38	36	40	1.1	27	27	24	31	1.5
Prepelvic scutes	16	16	14	18	0.8	16	16	13	18	0.9
Postpelvic or preanal scutes	12	12	10	16	1.1	12	13	10	14	1.0
Dorsal fin rays	15	15	13	17	0.8	15	15	14	18	0.8
Anal fin rays	15	16	14	16	0.7	15	15	13	19	1.0
Morphometric measures in thousandths of the standard length										
Cephalic length	239.3	225.4	185.7	271.2	14.4	237.7	250.0	208.3	269.2	10.6
Body depth	273.7	271.4	228.6	307.6	16.9	298.1	300.0	270.3	356.6	12.6
Predorsal length	442.5	438.6	338.7	491.6	20.7	440.2	423.7	400.0	475.0	18.9
Preanal length	754.1	746.5	677.4	885.7	34.6	749.4	721.3	694.9	902.8	30.7
Caudal peduncle length	122.9	121.2	101.6	157	11.5	128.4	125.0	101.7	151.4	10.4
Caudal peduncle depth	114.4	113.6	97.4	128.8	7.1	123.1	125.0	106.7	137.4	6.7
Pelvic fin length	127.4	136.4	103.7	145.2	9.2	130.5	125.0	117.6	146.2	7.3
Pectoral fin length	183.3	183.1	134.3	213.1	13.4	179.6	169.5	157.8	202.7	10.2
Preorbital length	62.2	70.4	46.3	78.7	6.7	63.8	67.8	51.3	75.5	6.2
Postorbital length	94.0	100.0	64.0	136.0	10.3	95.5	100.0	77.4	109.1	7.0
Eye diameter	81.0	85.7	59.2	99.4	7.3	84.9	84.8	70.6	105.3	6.3
Pupil diameter	43.3	45.5	35.1	57.1	5.0	47.4	50.9	36.5	60.0	6.4
Interorbital distance	62.3	57.1	40.3	85.4	10.7	73.6	67.8	61.0	90.9	5.4
Upper jaw length	105.6	100.0	61.4	121.4	9.3	105.9	101.7	87.7	121.1	6.1

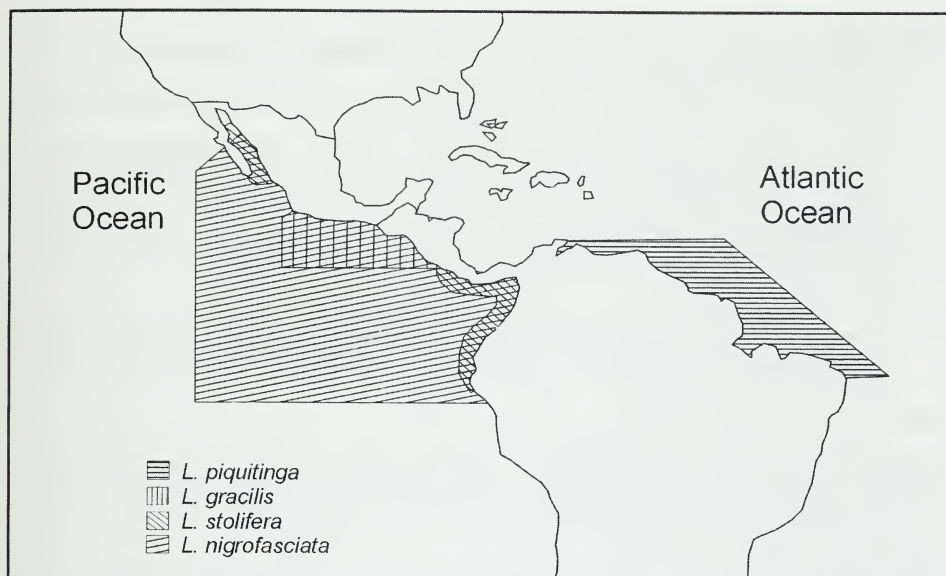


Fig. 6. Distribution ranges of the species of the genus *Lile* in tropical America.

to carry out finer studies to understand the evolutionary processes that gave origin to *L. gracilis*, the species that replaces *L. stolifera* in the central part of the tropical eastern Pacific.

Acknowledgments

We wish to thank the following persons and institutions for the facilities and assistance provided during the present study: José De La Cruz-Agüero and Adrián González-Acosta from Ichthyological Collection of CICIMAR-IPN, for providing help during the examination of specimens utilized in the description of this new species. Liduvina Pérezgomez from Laboratory of Morphophysiology (CICIMAR-IPN), for assisting in the process of clearing and staining of the specimens utilized in the osteological analysis. CIBNOR's Arachnology & Entomology Laboratory for providing the camera lucida for drawing the fish bone sketches and to the Ichthyological Collection of CIBNOR for providing part of the type material supporting this study. Oscar Armendáriz (CIBNOR) for making the final edition of the fish bone drawings. William N. Eschmeyer and Tomio Iwamoto from the Department of Ichthyology of the California Academy of Sciences in San Francisco for the loan of specimens for this study. Jeffrey A. Seigel from the Natural History Museum of Los Angeles County, in Los Angeles for the access to database and specimens. Salvador Contreras-Balderas from Bioconservación A.C., in Monterrey (México) for providing the southernmost record of *L. gracilis*. Daniel A. Guthrie and two anonymous reviewers provided useful comments and editorial help on the manuscript. Finally, Faustino Camarena-Rosales (UABC) for assisting in the statistical analysis of morphometric data.

Literature Cited

Balart, E.F. 1985. Development of the vertebral column, fins and fin supports in the Japanese anchovy, *Engraulis japonicus* (Clupeiformes, Engraulididae). *Bull. Mar. Sci.*, 56: 495-522.

- Castro-Aguirre, J.L., and J.M. Vivero. 1990. Existencia de una nueva especie del género *Lile* Jordan y Evermann (Osteichthyes: Clupeidae) en la costa occidental del Pacífico mexicano. *An. Esc. Nac. Cien. Biol., México*, 33: 135–146.
- Castro-Aguirre, J.L., H. Espinosa Pérez, and J.J. Schmitter-Soto. 1999. Ictiofauna estuarino-lagunar y vicaria de México. Noriega-Limusa, México, D.F. 711 pp.
- Chirichigno F, N. 1963. Estudio de la fauna ictiológica de los esteros y parte baja de los ríos del Departamento de Tumbes [Perú]. Servicio de Pesquerías, Perú, Ser. Divul. Cient., 22: 1–87.
- Gómez-Gaspar, A. 1976. Osteología de *Lile piquitinga* (Schreiner and Miranda-Ribeiro 1903) (Pisces: Clupeidae). *Bol. Mus. Mar, Univ. de Bogotá*, 8: 3–52.
- Matsuoka, M. 1998. Osteological development in the Pacific sardine, *Sardinops melanostictus*. *Ichthyol. Res.*, 44: 275–295.
- McGowan, M.F., and F.H. Berry. 1984. Clupeiformes: development and relationship. Pp. 108–126. *In*: Moser, H.G., W.J. Richards, D.M. Cohen, M.P. Fahay, A.W. Kendall, Jr., and S.L. Richardson (eds.). *Ontogeny and Systematics of Fishes*. American Society of Ichthyologist and Herpetologist, Special Publication No. 1.
- Vivero, J.M., and J. Romero-Castillo. 1990. *Lile gracilis* Castro-Aguirre y Vivero: un caso de especiación por neotenia. *Bol. Inst. Oceanogr. Venezuela, Univ. de Oriente*, 28 (1–2): 121–126.
- Whitehead, P.J.P. 1985. FAO species catalogue. Vol. 7. Clupeoid fishes of the world. An annotated and illustrated catalogue of the herrings, sardines, pilchards, sprats, anchovies and wolfherrings. Part 1. -Chirocentridae, Clupeidae and Pristigasteridae. FAO Fisheries Synopsis (125), Vol. 7, Pt. 1: x + 303.
- Yáñez-Arancibia, A. “1978” (1980). Taxonomía, ecología y estructura de las comunidades de peces en lagunas costeras con bocas efímeras del Pacífico de México. *Centro Cien. Mar y Limnol., Univ. Nac. Autón. México, Publ. Esp.*, 2: 1–306.

Accepted for publication 16 March 2001

Appendix 1. Other Material Examined:

- Lile nigrofasciata* sp. nov. Baja California Sur, México: Ensenada de La Paz at Manglar [Estero de] El Conchalito, CI: 4954, 30(57.5–85.0 mm), 16-17/IX/1997, A.F. González Acosta; Bahía Magdalena at Estero San Buto [24° 46' N, 112° 05' W], CI: 4560, 1(110.0 mm), 4/VI/1984, coll.?: Bahía Magdalena at Estero Las Botellas [24° 26' N, 111° 07' W], CI: 778, 1(77.0 mm), 10/XI/1985, U. McGregor; Bahía Magdalena at Estero San Carlos [24° 47' N, 112° 05' W], CI: 2279, 2(77.0–78.0 mm), 8/XI/1990, R. Rodríguez; Bahía Magdalena at Puerto Chale [24° 43' N, 111° 32' W], CI: 1861, 1(98.3 mm), 14/IV/1986, F. García; Bahía Magdalena at Estero Médano Amarillo [24° 43' N, 112° 02' W], CI: 1894, 4(87.0–96.0 mm), 11/III/1981, J.L. Castro Ortíz. Guerrero, México: Laguna de Tres Palos [15° 48' N, 98° 46' W], CI: 2282, 63(33.0–61.0 mm), 24/IV/1991, P.J.P. Whitehead et al. Tumaco, Colombia, CAS: 213293, 20 (49.0–82.5 mm), 1913, A. Henn & C. Wilson.
- Lile stolifera*. Baja California Sur, México: Ensenada de La Paz at Manglar El Conchalito, CI: 4738, 7(79.0–86.0 mm), 22-23/IV/1997, A.F. González Acosta; Estero de San José del Cabo [22° 55' N, 109° 46' W], CI: 3279, 58 (56.0–71.0 mm), 17/V/1989, P.J.P. Whitehead & R. Rodríguez; Bahía San Juanico at Punta Pequeña, LACM: 32084, 73 (45–64 mm), 28/X/1971, C. Swift; Bahía Concepción at Isla Anegada, CI: 1011, 36(53.0–74.0 mm SL), 12/VIII/1990, J. Rodríguez et al.; Río Santa Rosalía [=San Luciano], LACM: 50296, 4 (47–62 mm), 12/III/1957, G.W. Barlow; Río Mulegé at 2.1–3.0 km above the mouth, UABC: 0180, 2(47.7–61.7 mm), UABC: 0191, 3(46.2–50.7 mm), UABC: 0204, 1(47.7 mm), 14/X/1995, G. Ruiz-Campos. Nayarit, México: Estero San Blas, LACM: 50485, 1(86 mm), 30/I/1958, B.W. Walker et al. Puerto Parker, Costa Rica, CAS: 146862, 10(54.0–73.5 mm), 12-22/I/1938, W. Beebe et al.
- Lile gracilis*. Guerrero, México: Mouth of the Río Balsas (La Barra de San Francisquito), ENCB-IPN: 7134, 6(53.0–74.0 mm), 24/II/1988, A. Marmolejo; and Río Balsas at Brazo de San Francisquito, CIB: 2501, 5(35.6–67.6 mm), 6/X/1993, F. de Lachica-Bonilla et al.